Hubert, J. & Savill, P. (1999) Improving Oak: the first steps towards a breeding programme.
Quarterly Journal of Forestry. **93**(2): 117-125.

IMPROVING OAK: THE FIRST STEPS TOWARDS A BREEDING PROGRAMME

by JASON HUBERT* and PETER SAVILL*

SUMMARY

A genetic improvement programme for oak (*Quercus robur* and *Q. petraea*) has begun and selection of trees has been completed. Criteria were chosen to maximise recoverable timber volume and quality, with an emphasis on improving form and reducing shake. The 246 trees selected were reduced to 110 using primarily the criterion of vessel size. The larger vessel sizes were in Dutch oak; planting this material could increase the predisposition to shake. A poor acorn crop in 1998 meant that collection will be repeated in 1999. Shoots were collected in early 1999 for grafting and propagation, in collaboration with Horticulture Research International.

Introduction

The long-term nature of the genetic improvement of temperate broadleaved trees, coupled with the highly-variable timber quality of many native hardwoods, has led to a reluctance to fund breeding projects which have a projected lifetime of more than 40 years. Hence, our understanding of the genetics of these species is limited and attempts to improve them have only recently started, under the umbrella of the British Hardwoods Improvement Programme (Savill, 1998). In the Netherlands, improvement in oak has been achieved by selection but with no real trials. In the UK, the Forestry Commission is running oak progeny and provenance trials but has not selected elite trees with a view to a breeding programme. This project is unique in that it is the only programme for oak which combines all the elements of selection, trial and breeding.

Oak presents a problem due to the length of time until its sexual maturity and the low quantities of seed produced per hectare, hence the need to combine breeding and vegetative propagation. Horticulture Research International has extensive experience in the breeding, improvement and propagation of fruit trees and has been collaborating with the Oxford Forestry Institute in the oak project.

The method used is to collect seeds from selected mother trees and use them to establish breeding seedling orchards. This concept combines a trial and a seed orchard (Barnes 1986, 1995). The trial element will help to establish the genotypic contribution towards the observed elite phenotypes. Trees which do not perform well will be removed, leaving only the best for propagation which could be by sexual or vegetative methods. Micropropagation alone relies solely on phenotypic selection and removes the possibility for further genetic gains but can rapidly provide good planting stock.

For these reasons, we have decided to follow the slower route of breeding, but in conjunction with micropropagation. In this way, the superior material selected in the trials can be made available to growers in a shorter time than by breeding alone. In addition, due to the low seed output of oak per hectare, some form of scaling up will

* Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, South Parks Rd, Oxford OX1 3RB.

Peter Savill is reader in forestry at the University of Oxford. He has special interests in silviculture and tree improvement. Jason Hubert is a post-doctoral research officer in forestry working on the selection and acorn collection stages of the oak improvement programme.

be necessary to disseminate the improved material and, when improved seed is available, large-scale methods of vegetative propagation will be needed.

Objectives

The two principal objectives of this project are, first, to increase the recoverable timber production of oak per hectare by genetic means and, second, to increase the quality of the timber produced. If successful, then secondary environmental and amenity benefits could be expected to accrue, linked to an increase in the area of lowland broadleaved tree cover.

More immediate objectives from the collaboration with HRI are that the elite trees identified at the start of the project would be conserved *ex situ*, for possible vegetative propagation of superior clones and future genetic improvement programmes. They could eventually be compared with their progeny for inheritance studies, including the use of molecular markers for genetic mapping and for breeding commercially valuable selections.

Outline of Methods

Savill (1998) has outlined the breeding seedling orchards methodology adopted. It has shown itself to be cheaper than more complex breeding methods but still capable of producing large genetic gains in the improved material (Kanowski, 1993). One big advantage for the UK, where land prices are so high, is that it combines the trial and the seed orchard on to one site.

Selection

The first step is the selection of the best possible mother trees, whose progeny will make up the initial breeding population.

Great Britain, Ireland, northern France and the Netherlands were chosen as the range for selection since they encompass the climatic and geographic conditions encountered in Great Britain and Ireland. One concern is the potential for hybridisation between *Quercus robur* and *Q. petraea*. There is still debate as to the exact taxonomic status of these species and some authors treat both as one complex (Kleinschmit *et al*, 1995; Aas, 1993). Since the main objective of this project is timber production and the timber from either is indistinguishable, we have identified the selected trees but have chosen to treat both as one species for the purpose of selection and the trials.

The basis for selection in the field was phenotypic; the trees had to fulfil the criteria outlined below. Savill and Kanowski (1993) have discussed these characteristics in detail for oak. A minimum of around 50 trees is necessary to establish a sufficiently broad genetic base. Our aim was to select 200 suitable trees, with the intention of eliminating 100 and testing the remaining 100 in trials. The basis of elimination was wood properties, which are discussed later.

The selection criteria can be grouped into three broad categories:

(i) form

• straight stem. The first 6 m of each tree was ranked for straightness using the method of Barnes and Gibson (1986). In addition, the length of first-grade timber, total height, canopy length and the length of straight stem, regardless of branches (apical dominance), were measured.

• absence of fluting
• absence of spiral grain
• absence of basal sweep. This was not at all common in the stands visited, one exception being the Forêt Domaniale de Vouille, Poitiers, France, where there is a high proportion of oak of coppice origin.
• epicormics. The coverage of epicormics, where they occurred, was estimated as a percentage surface area on the worst affected side of the tree. Greater than 5 per cent coverage could be rejected by eye. Trees were selected with no epicormics or less than 1 per cent coverage. This criterion proved to be the most contentious due to the role of silviculture. However, even in stands with a high prevalence of epicormic shoots, some oaks do not produce them, which indicates a genetic contribution to their production. Research at Oxford University has shown that epicormic production is heritable (0.38, narrow sense), which indicates that it is possible to breed against epicormic production (Savill and Kanowski, 1993; Jensen *et al*, 1997).

(ii) health and vigour
• frost cracks. Trees with frost cracks were rejected.
• pests and diseases. Healthy trees with well developed crowns were selected, and occasionally trees which showed signs of die-back since this may be a function of the recent drought rather than a pathogen.
• dominant trees. Forest-grown trees were preferred over parkland trees, often on the basis of form, but also because the competitive environment in a forest stand has meant a higher selection intensity over the lifetime of the tree.

(iii) wood properties
The final selection of 100 trees was made on the basis of the criteria outlined above coupled with an examination of the number of sapwood rings (selection was based on low numbers of sapwood rings), and reduced susceptibility to 'shake', which is linked to average early-wood vessel diameters. Work by Savill (1986) has shown that oaks with large early-wood vessels (>160 microns radius) appear to have a much greater predisposition to shake than trees with smaller vessels (<145 microns radius). Subsequent work indicated that both vessel size (Savill and Mather, 1990; Kanowski *et al*, 1991; Savill *et al*, 1993b) and the number of sapwood rings (Savill *et al*, 1993a) are highly heritable. Both were measured from 5 mm diameter increment cores taken from near the bases of the trees.

Application of Criteria
Selection proceeded in two stages, with the criteria being applied in the order given above. Form and health were overriding; an eye-catching straight stem was often the first step towards the tree being selected. Some 246 trees were selected and these were reduced to 110 by rejecting those with above-average early-wood vessel diameters combined with a review of all other characters. The aim was to have good-quality trees and a geographical spread to capture diversity; for this reason no more than one tree was selected from any stand.

Finding the Trees
One of the problems of any selection programme is the time and expense taken to locate plus trees. For a tree as common as oak this problem is particularly difficult; a

complete survey would be impossible and unnecessary. The selections can not, therefore, be said to be the 100 best trees in the four countries visited, since not all were seen, but they do represent a good proportion of the best-quality oaks which exist in Great Britain and Ireland. In France and the Netherlands, selection was less intense but was guided by the local state forestry organisations to find the best material for planting in Great Britain and Ireland.

In Great Britain, three methods were used to sample both private- and state-owned woodlands:

• relocating the 'plus' trees selected by the Forestry Commission in the 1950s; 18 trees were selected from the 31 located.

• visiting the registered seed stands of oak; all but three of the 63 stands contained in the 1997 Great Britain list of stands were visited.

• letters were placed in several journals (for example, Barne, 1998) which forestry professionals and landowners read. Replies to these proved to be very useful. This method was preferred to a more general article in a national newspaper.

In Ireland, visits were undertaken to plus trees already identified for Coillte Teoranta (the Irish Forestry Board). In addition, several stands which had shown good results in trials of native material were visited. Efforts were made to sample across the whole country but the quality of the oak declined towards the west. The majority of stands visited were state owned. All three of the registered stands of oak in Northern Ireland were visited, as were trees on three private estates.

Registered seed stands of French oak were recommended by the Centre National du Machinisme Agricole, du Génie Rural, des Eaux et des Forêts for planting in the UK. These were located predominately in north-west France. In addition, two stands were included which would represent the southern (Poitiers) and the continental eastern limit (Fontainebleau) for oak which would be expected to perform well in the UK. All the stands visited were owned and managed by the Office National des Forêts.

In the Netherlands, the top 15 registered and tested seed stands of oak recommended by the Instituut voor Bos- en Natuuronderzoek were visited. All these seed stands were roadside avenues owned by different state and private owners.

Selection Intensity

To give an idea of the level of selection it is useful to provide an approximate estimate of the selection intensity. The average size of the wood/compartment visited was estimated at 5 ha and the assumed stocking density is 70-100 trees/ha. In total, 235 woods/compartments were visited and 110 trees selected for trial. This gives an estimated selection intensity of 0.14-0.09 per cent, or about one tree selected in 1,000.

Distribution and Range of the Selected Trees

The distribution of selected plus trees by country and species is given in Table 1. The proportions of *Quercus robur* and *Q. petraea* are governed by the geographical extent of the search, with predominately more *Q. robur* in the east and more *Q. petraea* in the west. The fact that the proportions of each species in the initial selection are roughly equal to the proportions of each in the final selection indicates that there was no correlation between vessel size and species for *Q. robur* and *Q. petraea*. This was borne out by statistical analysis.

Table 1: Distribution of selected oak plus trees by species and country.
Initial selections are bracketed; the final selections are not.

country	*Q.robur*		*Q.petraea*		*unknown/hybrids*		*total*	
Great Britain	(93)	44	(55)	22	(12)	4	(160)	70
France	(5)	3	(37)	14	(0)	0	(42)	17
Ireland	(8)	4	(11)	7	(1)	1	(20)	12
the Netherlands	(24)	11	(0)	0	(0)	0	(24)	11
total	(130)	62	(103)	43	(13)	5	(246)	110

A map showing the distribution of the selected plus trees is shown in Figure 1. The geographical spread is a north-south range of approximately 1,200 km and an east-west range of 960 km. This encompasses the variation of climatic and soil conditions which oaks are likely to encounter in Great Britain and Ireland.

Wood Properties Results

A summary of the wood properties data is given in Table 2. The two selection criteria – mean vessel size and the number of sapwood rings – were very weakly correlated (Pearson Correlation coefficient = -0.232) and, therefore, selection for both criteria would have required a much larger initial sample than was available. Since shake is a more serious problem than the proportion of sapwood, the mean vessel size was used as the main selection criterion and where possible sapwood rings were included. Only for the British oaks was there a statistically significant difference (at $P<0.05$) between the mean vessel size of the finally-selected trees and the initially-selected trees. The small sample size elsewhere may explain the lack of a statistically significant difference.

Figure 2 shows that on a country basis the French and Irish selections have significantly smaller mean vessel sizes than the British or Dutch oaks. The Dutch

Table 2: Mean vessel size, number of sapwood rings, average age and radial growth for the last 10 years for the initial and final selections.

	Great Britain mean (SD)		*France* mean (SD)		*the Netherlands* mean (SD)		*Ireland* mean (SD)	
	initial	final	initial	final	initial	final	initial	final
number[1]	154	68	34	15	24	11	20	12
mean vessel radius, µm[2]	159.6^{a} (19.96)	149.9^{c} (13.94)	145.6^{bc} (20.15)	132.0^{b} (10.25)	179.4^{d} (16.64)	168.8^{ad} (10.10)	141.4^{bc} (16.34)	131.9^{b} (10.52)
number of sapwood rings[2]	23.1^{a} (6.36)	23.9^{a} (6.95)	25.0^{a} (6.15)	24.0^{a} (5.75)	16.0^{b} (4.59)	15.7^{b} (4.56)	23.6^{a} (4.84)	22.6^{ab} (4.50)
average age, yr[2]	151^{a} (59.6)	152^{a} (64.8)	202^{b} (59.7)	216^{b} (75.0)	102^{c} (36.4)	101^{ac} (39.5)	104^{c} (51.2)	103^{ac} (54.7)
10-year radial growth, mm[2]	26.0^{b} (10.7)	23.9^{ab} (9.79)	20.3^{ab} (9.98)	16.5^{a} (6.58)	44.7^{c} (17.27)	44.36^{c} (16.98)	25.3^{a} (13.3)	23.5^{ab} (7.27)

[1] Number of trees in the sample. Note: wood samples were not available for all the selected trees.
[2] For each character, values with the same letter are not significantly different by Tukey's Pairwise comparison at $P<0.05$.

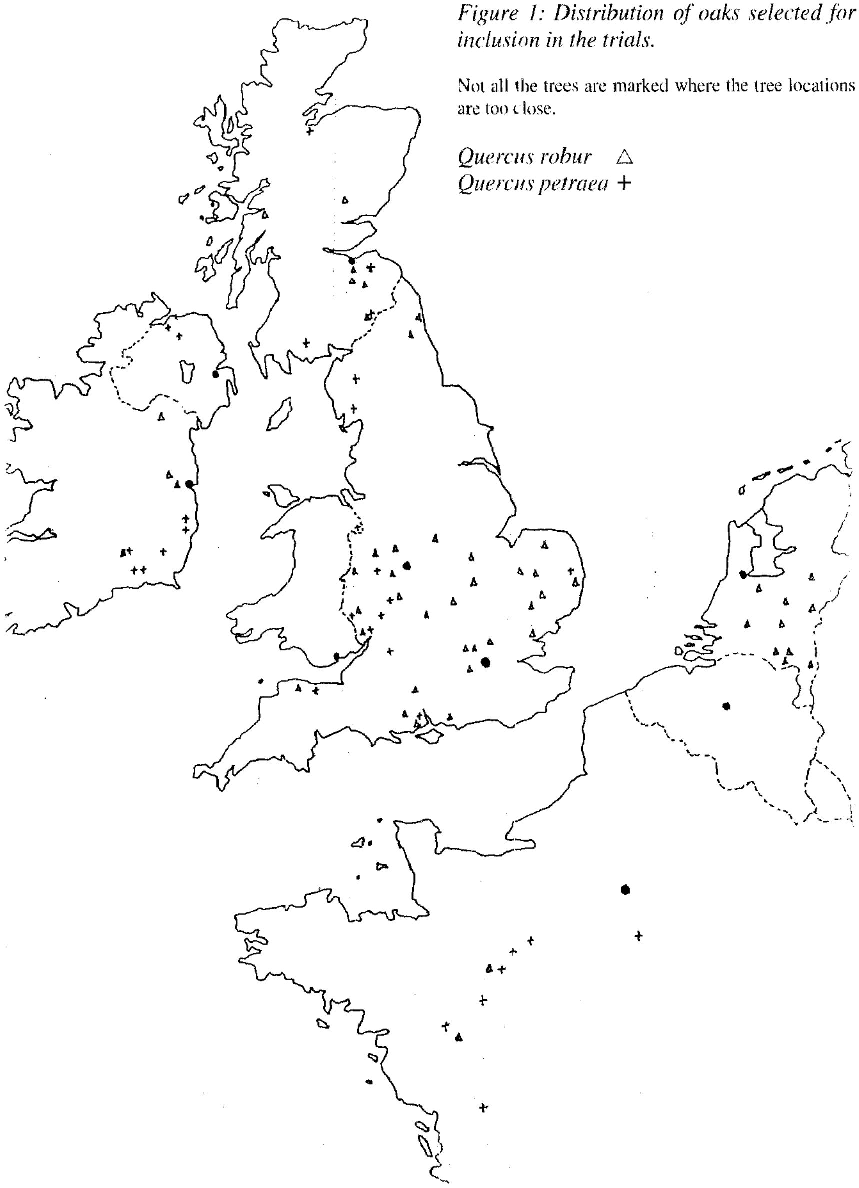

Figure 1: Distribution of oaks selected for inclusion in the trials.

Not all the trees are marked where the tree locations are too close.

Quercus robur △
Quercus petraea +

oaks have the largest mean vessel sizes, significantly larger than the British selections. This could have important consequences for British forestry since Dutch oak is commonly planted in Britain yet the larger vessel sizes indicate an increased propensity to shake. Work by Savill and Mather (1990) has shown that vessel size is also related to flushing date. Therefore, the country variation may be due to the milder climates of Ireland and western France favouring early flushing dates, and hence smaller vessel sizes; whereas the more continental climate of the Netherlands,

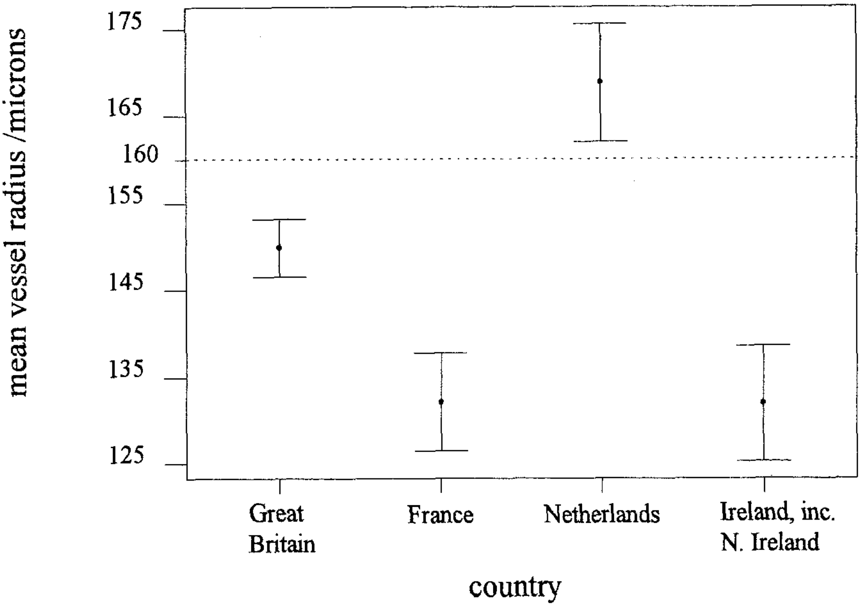

Figure 2: Mean vessel radii of selected trees for each country.

Bars show 95 per cent confidence intervals for the means. Mean radii greater than 160 microns are prone to shake (Savill, 1986).

with the possibility of late frosts, favours later flushing and hence larger vessel size.

Radial growth over the past 10 years was recorded to test whether it is correlated with any other observed traits. Correlations were generally poor, with Pearson correlation coefficients greater than 0.4 only being found between radial growth and age (R=-0.404), mean vessel size (R=0.416) and sapwood rings (R=-0.581).

The negative correlation observed between growth and age is to be expected, since mature trees grow more slowly in diameter than younger trees. The fact that the correlation is so poor indicates the large influence of silviculture and environment on growth.

The correlation with vessel size is counter intuitive, since mean vessel size within a tree is constant and unaffected by speed of growth. However, when the data are examined on a country-by-country basis the fact that the fastest-growing trees are in the Netherlands, where they are open grown, and the slowest in France, where the trees were grown at high stocking densities, indicates that the correlation is fortuitous and due to differing silvicultural systems, plus the country differences outlined above for vessel size. When the correlation coefficient is recalculated using only samples from Great Britain it drops to 0.25, indicating that this is the case.

For sapwood, there is a relatively large negative correlation between the number of sapwood rings and diameter growth. The reason for this is unclear but it could be linked to the physiology of heartwood formation.

The Next Steps

In 1998, there was a very poor acorn crop everywhere except the Netherlands. In the Netherlands, there was a mast year and collections were obtained for all the selected trees. In addition, a few collections have been successful in the UK. We are planning to repeat collections in 1999 in the hope of a better crop. Acorns which have been collected will be sown in the Forest Commission Research Agency's nursery in Roslin.

In collaboration with HRI, a collection of vegetative material from all the selected plus trees will begin in 1999. These will be grafted on to clonal rootstocks currently being developed to provide a collection of genetic material from all the mother trees, allowing the possibility of future genetic analysis. This technique has been used by HRI to assess the performance and growth form of fruit trees for many years (Howard, 1987, 1995) and has been achieved for oak propagated from mature trees at East Malling (Marks and Simpson, 1993). The technique also allows the rapid propagation of material for screening; one potential application is screening for oak mildew resistance.

The clonal propagation of oak is difficult both by conventional vegetative cuttings and by micropropagation. However, HRI propose to investigate the feasibility of vegetatively propagating 20 elite trees on their own root systems both by micropropagation and vegetative cuttings, with the aim of answering the question, can mature oak be reliably micropropagated?

Acknowledgements

We would like to thank the following organisations for funding during 1998: Dulverton Trust, Scottish Forestry Trust, Woodland Heritage, Leverhulme Trust, Coillte Teoranta, Sotterley Farms, Northern Ireland Forest Service and the Forestry Authority.

In addition, we would like to thank the many forest managers and owners in the four countries who gave freely of their time and expertise. In particular, John Fennessy of Coillte Teoranta, Jean-Marie Allouard of the ONF and Gert Kranenborg of IBN-DLO, who all provided enormous help during visits to their respective countries.

REFERENCES

Aas, G. (1993). Taxonomical impact of morphological variation in *Quercus robur* and *Q. petraea*: a contribution to the hybrid controversy. *Annales des Sciences Forestières* **50**, Suppl 1, 107s-113s.

Barne, M. (1998). Have you seen a good oak lately? *Quarterly Journal of Forestry* **92**(1), 54.

Barnes, R.D. (1986). Multiple population tree breeding in Zimbabwe. In *Proceedings IUFRO Joint Meeting of Working Parties on Breeding Theory, Progeny Testing and Seed Orchards.* Williamsburg, VA, USA, 13-17 October 1986, 285-297.

Barnes, R.D. (1995). The breeding seedling orchard in the multiple population breeding strategy. *Silvae Genetica* **44**(2-3), 81-88.

Barnes, R.D. and Gibson, G.L. (1986). A method to assess stem straightness in tropical pines. *Commonwealth Forestry Review* **5**(2), 168-171.

Howard, B.H. (1987). Propagation. In *Rootstocks for Fruit Crops* edited by R.C. Rom and R.F. Carlson. Wiley, New York, pp 29-77.

Howard, B.H. (1995). Opportunities for developing clonal rootstocks from natural seedlings of *Tilia* spp. *Journal of Horticultural Science* **70**(5), 775-786.

Jensen, J.S., Wellendorf, H., Jager, K., De Vries, S.M.G. and Jensen, V. (1997). Analysis of a 17-year old Dutch open-pollinated progeny trial with *Quercus robur* (L.). *Forest Genetics* **4**(3), 139-147.

Kanowski, P.J. (1993). Forest genetics and tree breeding. *Plant Breeding Abstracts* **63**(6), 717-726.
Kanowski, P.J., Mather, R.A. and Savill, P.S. (1991). Short note: Genetic control of oak shake; some preliminary results. *Silvae Genetica* **40**(3/4), 166-168.
Kleinschmit, J.R.G., Bacilieri R., Kremer, A. and Roloff, A. (1995). Comparison of morphological and genetic traits of pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.). *Silvae Genetica* **44**(5/6), 256-269.
Marks, T.R. and Simpson, S.E. (1993). Changes in the competence of *Quercus robur* 'Fastigiata' to grow *in vitro* as affected by seedling rootstocks and differential pruning. *Journal of Horticultural Science* **68**, 815-824.
Savill, P.S. (1986). Anatomical characters in the wood of oak which predispose trees to shake. *Commonwealth Forestry Review* **65**, 109-116.
Savill, P.S. (1998). British Hardwoods Improvement Programme. *Quarterly Journal of Forestry* **92**(3), 217-222.
Savill, P.S. and Kanowski, P.J. (1993). Tree improvement programmes of European species: goals and strategies. *Annales des Sciences Forestières* **50**, Suppl 1, 368s-383.
Savill, P.S. and Mather, R.A. (1990). A possible indicator of shake in oak: relationship between flushing dates and vessel sizes. *Forestry* **63**, 355-362.
Savill, P.S., Kanowski, P.J., Gourlay, I.D. and Jarvis, A.R. (1993a). Short Note: Genetic and intra-tree variation in the number of sapwood rings in *Quercus robur* and *Q. petraea*. *Silvae Genetica* **42**(6), 371-375.
Savill, P.S., Mather, R.A. and Kanowski, P.J. (1993b). Struggling with shake: the recognition of shake-prone oaks. *Timber Grower* **128**, 28-29.

SECURING OUTLETS FOR BROADLEAVED TIMBER IN SOUTH-EAST ENGLAND

South-east England used to enjoy a ready local market for timber. But the market and prices paid for small-diameter broadleaved roundwood have both declined markedly over the past 50 years. This decline has accelerated over the 1990s. It has been caused partly by the global trend towards larger timber-processing plants, which has led to the closure of local traditional small sawmills; the South-East has not benefited from the new processing lines and expansions to existing capacity which have taken place in some parts of the UK. Alongside this are the current increases in recycling and the use of residues, which continue to reduce the demand for round timber.

The loss of demand by regional processors is seen as a major challenge to the rural economy. This must be addressed and resolved if broadleaved woodlands are to be sustainable managed and incomes improved throughout the wood chain. There has been concern that the South-East's woodlands – and the businesses and jobs which they support – would be neglected and deteriorate as owners lost the financial incentive to continue managing them. As a result, the Forestry Commission, supported by the industry, engaged consultants – John Clegg & Co and Firn